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9.—South-western Australian occurrences of Sthenurus (Marsupialia, Macropodidae), including Sthenurus brownei sp. nov.

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Abstract

Specimens of *Sthenurus* from Mammoth Cave in the south-west of Western Australia have been re-examined and shown to fall into two groups, one with lower permanent premolars exceeding 16 mm in length, the other with lower permanent premolars less than 16 mm in length. These two groups are interpreted as distinct species rather than as sexual morphs. One of the species is *Sthenurus occidentalis* Glauert 1910, and a revised concept of this species is presented. The other species is newly described under the name *Sthenurus brownei*. The horizontal ramus of the mandible in *S. brownei* is much deeper behind M_4 than below the P_4-M_1 interspace, in contrast with any other described species of *Sthenurus* in which mandibular form is known.

Both *S. occidentalis* and *S. brownei* are shown to occur in Strong's Cave, near Mammoth Cave, and *S. brownei* is shown to occur also at Wanneroo, near Perth.

Introduction

While examining specimens of *Sthenurus* from Mammoth Cave, Western Australia, I became aware that two forms could be distinguished on the morphology and size of the lower permanent premolars and the lower incisors. Size and morphology of other teeth in these two forms were very similar. I have examined two alternative reasons for the observed incisor and premolar differences, namely sexual dimorphism and specific difference. Marked differences in many non-dental characters, and less marked differences in upper incisors, upper permanent premolars, upper molars and lower molars lead me to conclude that two different species of *Sthenurus* are represented in the Mammoth Cave sample.

Up to this time, the Mammoth Cave sample of *Sthenurus* has been assumed to represent only one species (*S. occidentalis* Glauert 1910), and other species of *Sthenurus* have been defined partly by comparison with this supposedly homogeneous sample from Mammoth Cave, as for example *S. oreas* by Bartholomai (1963) and *S. oreas* and *S. orientalis* by Tedford (1966). I have therefore thought it desirable to describe the differences between the two Mammoth Cave species in some detail.

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Both species represented in the Mammoth Cave sample appear also to be represented in deposits in Strong's Cave (about 7 miles S. of Mammoth Cave), while the species newly described from Mammoth Cave appears also to be present at Wanneroo, in the Perth metropolitan region.

A *Sthenurus* premolar, probably representing *S. gilli* Merrilees 1965, is known from Madura Cave on the Nullarbor Plain (Lundelius 1963), and this occurrence has been discussed previously (Merrilees 1965). *Sthenurus* is also reported from the Balladonia district, on the western margin of the Nullarbor Plain (Glauert 1912). Neither of these occurrences is further considered in the present paper, which is confined to occurrences of *Sthenurus* in the South West Division as delimited by the 1966 edition of the Geological Map of Western Australia issued by the Geological Survey of Western Australia (Mines Department, Perth).

Copies of raw data on tooth dimensions in the south-western Australian samples of *Sthenurus* described herein have been lodged in the libraries of the Western Australian Museum (Beaufort St., Perth), the National Museum of Victoria (Russell St., Melbourne C1) and the Queensland Museum (Gregory Terrace, Brisbane). For statistical purposes, each individual animal has been represented only once for each dimension (see note, Merrilees 1965 p.24); all teeth were measured at the crowns, and all measurements were maximal, save that "width" in molars was measured across the protoloph (id). "Depth" in lower incisors represents a measurement perpendicular to the long axis of the tooth. Data have been tabulated in the same form as used in previous discussions of relatively large samples of *Sthenurus* by Marcus (1962) and Merrilees (1965).

There is an unfortunate confusion in premolar tooth nomenclature in the macropodids, introduced by Stirton (1955) and followed by several other writers, e.g. Marcus (1962); Lundelius (1963); Bartholomai (1963); Tedford (1966). Tedford (1966) in his review of *Sthenurus* sets out his reasons for adopting this new nomenclature to replace the older nomenclature, established by

Oldfield Thomas (1887) and adopted by nearly all later writers on marsupials. It appears that both systems are based prematurely on matters of tooth homology at present little understood either from embryological or from palaeontological studies. To facilitate comparison of reports using opposing systems of premolar designation, I have used vernacular names wherever convenient. Thus I refer below to the "deciduous premolars" ($P^3/_3$ on the Thomas nomenclature, $P^2/_2$ on the Stirton nomenclature) the "milk molars" (Thomas' $DP^4/_4$, Stirton's $DP^3/_3$) and the "permanent premolars" (Thomas' $P^4/_4$, Stirton's $P^3/_3$). However, where these circumlocutions are not convenient, I have retained the older Thomas nomenclature (see Thomas 1922, Ride 1964).

By courtesy of the curators of the fossil collections in other Australian museums, I have been able to make direct comparisons between the Mammoth Cave specimens and specimens of *S. atlas* from Wellington Caves (Aust. Mus. Syd. F 29556, 29558, 29575, 29582, 29584, 29585, 47052, 47059, 47063 and W. Aust. Mus. 66.10.11, cast of holotype), *S. andersoni* from King's Creek, Darling Downs (Qd. Mus. F 3813), *S. antiquus* from the Darling Downs (Qd. Mus. F 2931 and 2932), *S. oreas* from Gore, Queensland (Qd. Mus. F 3814), and *S. gilli* from Strathdownie, Victoria and from Naracoorte, South Australia (the numerous Nat. Mus. Vict. and S. Aust. Mus. specimens listed by Merrilees 1965), as well as numerous specimens of less certain identity from other localities in N.S.W., Victoria, King Island, and South Australia. For other comparisons, I have relied upon the published descriptions, dimensions and illustrations cited below, and have allowed for large discrepancies between the measurements recorded under the same names (e.g. "lengths" of molars) by different observers, because there are no standardized methods of measuring marsupial teeth (cf. Tedford 1966).

The Mammoth Cave deposit

Mammoth Cave is in an outcrop of calcareous aeolianite in the south-western portion of Western Australia, between Capes Naturaliste and Leeuwin. Numerous remains of marsupials and other vertebrates have been collected from this cave, mainly by L. Glauert in the early years of the present century. The fossiliferous deposit appears to have been part of a talus fallen through holes in the roof of the cave; it is certainly older than 31,000 radiocarbon years B.P. (Tamers, Pearson & Davis 1964) and probably older than 37,000 years B.P. (Lundelius 1960), according to estimates of the age of charcoal samples collected recently from what little remains of the deposit. I have shown (Merrilees, Ph.D. dissertation) that the age of the aeolianite in which the cave is cut cannot exceed late Milazzian (Oakley 1964), that probably the age of the deposit in the cave does not exceed the early phases of the Last (Würm or Wisconsin) Glaciation, and that the whole fossiliferous deposit probably accumulated in a relatively short time.

The holotype of *Sthenurus occidentalis* was among the first (and hence presumably youngest) specimens collected from the Mammoth Cave deposit (Glauert 1910b). As holotype for the second *Sthenurus* species about to be described, I have selected a specimen which probably also came from the upper part of the deposit; the two holotypes must be of very nearly the same age.

The Sthenurus sample from Mammoth Cave

This consists of a great deal of material not bearing teeth, little of which has been studied or even catalogued, and 167 catalogued tooth-bearing specimens upon which the present paper is largely based. In addition Tedford (1966) reports the presence of 12 *Sthenurus* specimens from Mammoth Cave now in the Museum of Palaeontology, University of California, which I have not examined; there is at least 1 specimen in the Chicago Natural History Museum, of which I have a plaster cast (W. Aust. Mus. 63.5.15) kindly supplied by W. D. Turnbull, and 1 or more specimens in the American Museum of Natural History and in the British Museum (Natural History). Criteria by which specimens may be referred to the genus *Sthenurus* are set out by Tedford (1966).

Of the 167 tooth-bearing specimens from Mammoth Cave available to me, 5 are not specifically identifiable, 53 are referred to *Sthenurus brownei* sp. nov. and 111 are referred to *S. occidentalis* on grounds detailed below. All specifically determinable tooth-bearing specimens are listed with the raw data mentioned above.

At least 13 individuals of *S. brownei* and at least 16 individuals of *S. occidentalis* contributed to the Mammoth Cave sample available to me. Despite these substantial numbers of individuals, *Sthenurus* (even counting both species together) is not the most abundant macropodid in the Mammoth Cave deposit as stated by Tedford (1966 p.6); in numbers of individuals or of specimens, it is far exceeded by *Setonix* (more than 140 individuals).

Sthenurus brownei* sp. nov.

Sthenurus occidentalis (partim) Glauert, 1910, *Rec. West. Aust. Mus.* **1** : 31-36.

Holotype.—Western Australian Museum fossil vertebrate specimen 63.2.94, right mandibular ramus lacking upper portion of coronoid process, showing full adult dentition (i.e. I_1, P_4, M_{1-4}), ankylosed with small portion of left ramus showing damaged root of I_1 in alveolus. See Figures 1 and 2.

Type locality.—Mammoth Cave, Western Australia, 34° 1½′ S, 115° 1½′ E—Glauert excavation, north-central in cave.

Paratypes, same locality as holotype.—Portions of mandibles, W. Aust. Mus. specimens 63.2.39, 63.2.40 (+63.2.51), 63.2.41 (+ 63.2.48), 63.2.42 (+ 63.2.50), 63.2.43 (+ 63.2.46), 63.2.44, 63.2.81 (+ 63.2.49), 63.2.82, 63.2.89 (+ 63.2.95), 65.3.16, 66.9.43.

Other specimens referred to S. brownei, *same locality as holotype.*—

(a) Mandibular specimens 63.2.55, 63.2.63-64, 63.2.84, 63.2.105, 63.2.197, 65.3.15, 65.4.38, 65.12.5. Geological Survey of Western Australia specimen no. 10087—see Note by Glauert 1910b, p. 62.

* Named after I. A. and W. R. Browne, whose research and teaching respectively in palaeontology and Pleistocene events (among their other geological interests) have provided stimulus to many students including myself.

Fig. 1.—Holotype, *Sthenurus brownei*, Mammoth Cave, Western Australia Buccal view. Note tapering of ramus towards front, high masseteric crest, short masseteric fossa.

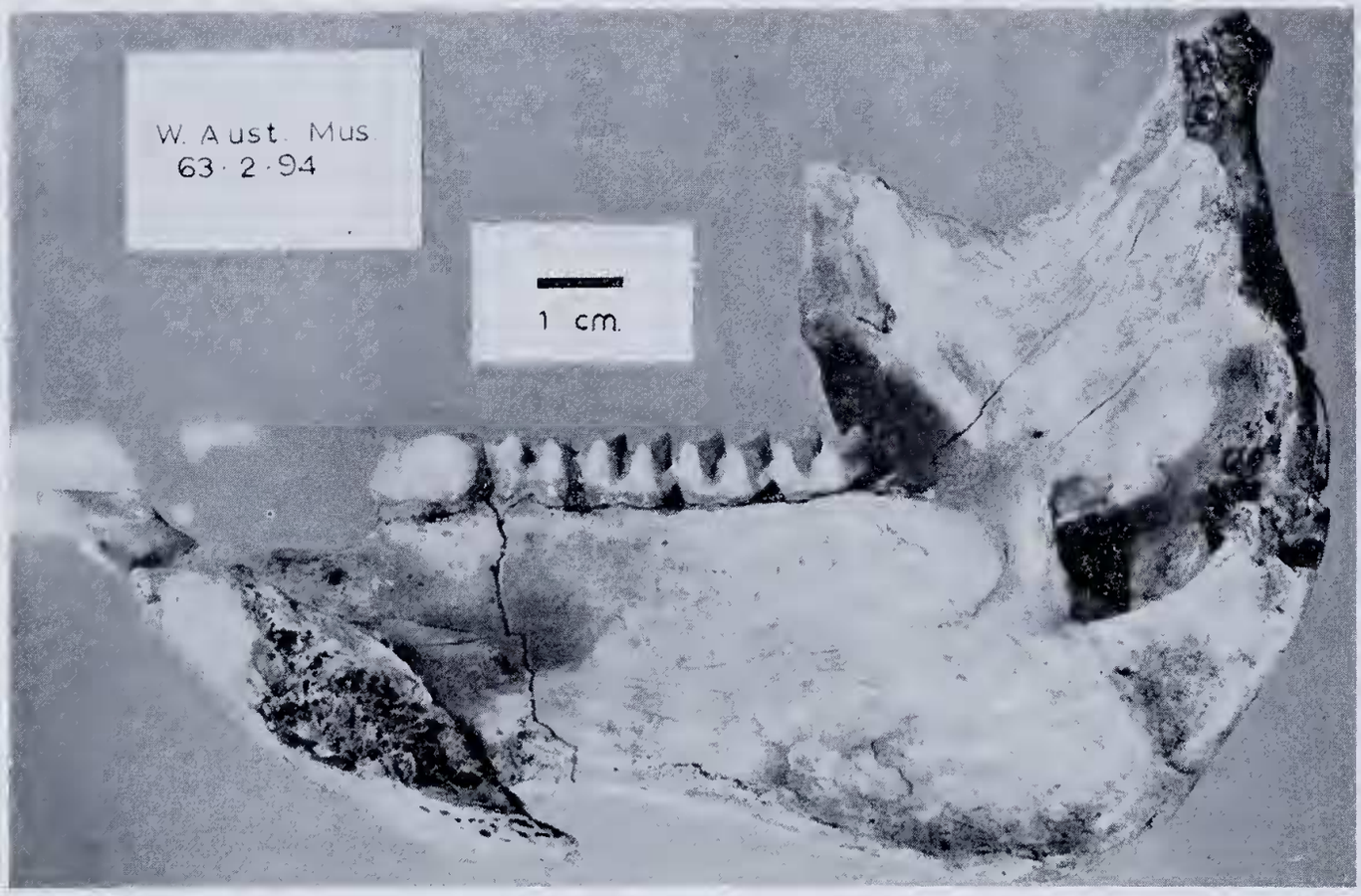

Fig. 2.—Holotype, *Sthenurus brownei*, Mammoth Cave, Western Australia. Lingual view. Note that crest bounding pterygoid fossa terminates in small sharp process.

(b) Maxillary and premaxillary specimens 63.2.116, 63.2.120, 63.2.124, 63.2.133, 63.2.135 (+ 63.2.141), 63.2.140, 63.2.145 (+ 63.2.144 + 63.2.148), 63.2.165, 63.2.167, 63.2.171, 63.2.174, 63.2.176, 63.2.179 (+ 63.2.143), 63.2.182, 63.2.185, 63.2.198, 63.5.8, 64.12.13, 65.4.36, 66.9.44-45. Cast 63.5.15.

(In the foregoing lists of specimens, numbers added in brackets refer to specimens catalogued separately but subsequently judged to derive from the same individual animal.)

Diagnosis.—Lower permanent premolar shorter than in *S.* occ*identalis*, but longer than longest (i.e. third) lower molar, and conspicuously longer than first lower molar. Lower incisor smaller than *S.* occ*identalis*, about same size as *S. gilli.*

Lower molars with well-marked posterior cingulum; about as wide at crest of protolophid as near base of enamel. Postero-buccal crest on lower permanent premolar extends further forward than mid-point of tooth before curving inward towards lingual crest.

Horizontal ramus of mandible much deeper behind M_4 than below P_4-M_1 interspace, giving mandible the appearance of tapering towards front; lowest part of masseteric crest nearly as high as alveoli of molars, and thin; masseteric fossa (level with top of mandibular foramen) conspicuously shorter antero-posteriorly than *S.* occ*identalis*; crest bounding pterygoid fossa terminates anteriorly in small sharp process. *Comparison of* S. brownei *with other species, and description.*—

TABLE 1

Tooth dimensions in Sthenurus brownei *from Mammoth Cave, Western Australia—holotype, paratypes, referred specimens.*

Upper

Dimensions Examined	Number of specimens Left	Number of specimens Right	Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation
Length deciduous premolar P^3		5	9.8—11.0	10.46	0.47	4.5
Width deciduous premolar P^3		4	9.4— 9.8	9.53	0.16	1.7
Length milk molar DP^4		5	9.5—10.5	10.00	0.37	3.7
Width milk molar DP^4		4	9.4—10.5	9.88	0.47	4.8
Length permanent premolar P^4	2	5	14.1—16.8	15.93	0.99	6.2
Width permanent premolar P^4	2	5	11.0—13.1	12.00	0.72	6.0
Length first molar M^1	6		10.2—11.4	10.80	0.46	4.2
Width first molar M^1	6		10.4—11.7	10.93	0.48	4.4
Length second molar M^2	7		10.6—12.0	11.40	0.48	4.2
Width second molar M^2	6		11.1—12.0	11.47	0.36	3.1
Length third molar M^3	6		11.5—12.1	11.80	0.27	9.9
Width third molar M^3	6		11.1—11.8	11.48	0.25	2.2
Length fourth molar M^4		3	10.9—11.5	11.27	0.32	3.2
Width fourth molar M^4		3	10.6—11.5	11.04	0.45	4.1

Lower

Dimension Examined	Holotype W. Aust. Mus. 63.2.94	Number of specimens (including holotype where relevant) Left	Number of specimens (including holotype where relevant) Right	Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation
Depth Incisor I_1	9.5		4	9.2—10.6	9.78	0.60	5.4
Length deciduous premolar P_3			5	8.7—9.2	8.92	0.19	2.1
Width deciduous premolar P_3			5	7.3— 8.1	7.78	0.33	4.2
Length milk molar DP_4			5	8.5— 9.6	9.20	0.46	5.0
Width milk molar DP_4		5		8.4— 8.8	8.52	0.09	1.1
Length permanent premolar P_4	14.7	3	7	13.2—15.3	14.42	0.60	4.2
Width permanent premolar P_4	9.9	3	8	9.0—10.0	9.64	0.38	3.9
Length first molar M_1	10.8	11		9.3—11.0	10.21	0.40	3.9
Width first molar M_1	9.2	10		8.6— 9.5	9.08	0.29	3.2
Length second molar M_2	11.5		9	10.5—11.5	11.09	0.36	3.2
Width second molar M_2	9.9		8	9.3—10.3	9.94	0.37	3.7
Length third molar M_3	12.0		7	11.1—12.1	11.57	0.39	3.4
Width third molar M_3	10.3		7	9.7—10.7	10.21	0.24	2.4
Length fourth molar M_4	11.2	4		11.1—11.5	11.33	0.15	1.3
Width fourth molar M_4	10.4		4	10.2—10.5	10.33	0.15	1.5

TABLE 2

Tooth dimensions in Sthenurus occidentalis *from Mammoth Cave, Western Australia—as revised.*

Upper

Dimension Examined	Number of specimens Left	Right	Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation
Length deciduous premolar P^3	4		10.5—10.8	10.68	0.15	1.4
Width deciduous premolar P^3	4		9.0— 9.7	9.42	0.30	3.2
Length milk molar DP^4	4		9.0—10.1	9.60	0.55	5.7
Width milk molar DP^4	4		10.2—11.3	10.63	0.50	4.7
Length permanent premolar P^4	5	7	16.9—18.8	17.58	0.61	3.5
Width permanent premolar P^1	6	7	11.8—13.9	12.73	0.58	4.6
Length first molar M^1		14	10.6—11.4	10.94	0.24	2.2
Width first molar M^1		15	10.6—11.5	11.11	0.98	8.8
Length second molar M^2		16	11.2—12.0	11.55	0.25	2.2
Width second molar M^2		14	11.4—12.3	11.86	0.28	2.3
Length third molar M^3		14	11.6—12.4	12.05	0.22	1.8
Width third molar M^3		16	11.5—12.7	12.13	0.35	2.9
Length fourth molar M^4		8	11.1—11.5	11.36	0.17	1.5
Width fourth molar M^4		7	11.3—11.9	11.69	0.22	1.9

Lower

Dimension Examined	Holotype W. Aust. Mus. 60.10.2	Number of specimens (including holotype where relevant) Left	Right	Observed Range mm	Sample Mean mm	Sample Standard Deviation mm	Sample Coefficient of Variation
Depth incisor I_1	13.3	9		11.8—13.3	12.41	0.46	3.7
Length deciduous premolar P_3		2		9.3— 9.8	9.55	0.35	3.7
Width deciduous premolar P_3		2		7.6— 8.4	8.00	0.57	7.1
Length milk molar DP_4		2		9.4— 9.6	9.50	0.14	1.5
Width milk molar DP_4		2		8.0— 9.4	8.70	1.04	11.9
Length permanent premolar P_4	16.8	12		16.3—17.6	16.74	0.36	2.2
Width permanent premolar P_4	9.7	12		9.7—10.7	10.14	0.36	3.6
Length first molar M_1	9.9		12	9.9—11.0	10.54	0.30	2.8
Width first molar M_1	8.8		13	8.8—10.1	9.45	0.39	4.1
Length second molar M_2	10.9	13		10.3—11.7	11.12	0.37	3.3
Width second molar M_2	9.4	11		9.4—11.3	10.34	0.57	5.5
Length third molar M_3	11.4		13	11.3—12.6	11.82	0.33	2.8
Width third molar M_3	10.1		13	10.1—11.6	10.88	0.31	2.8
Length fourth molar M_4	10.4	12		10.3—11.4	10.79	0.35	3.2
Width fourth molar M_4	10.2	11		10.2—11.3	10.56	0.36	3.4

Species with which *S. brownei* must be compared:—

S. atlas Owen 1838
S. andersoni Marcus 1962
S. notabilis Bartholomai 1963
S. tindalei Tedford 1966
S. occidentalis Glauert 1910
S. oreas De Vis 1895
S. pales De Vis 1895
S. antiquus Bartholomai 1963
S. orientalis Tedford 1966
S. gilli Merrilees 1965

See illustrations of *S. brownei*—Figures 1-3 (holotype and a paratype showing adult lower dentition and other diagnostic characters of the mandible), Figures 4, 5, 6 (showing probable upper dentition and skull characteristics) and Table 1 (summary of tooth dimensions in holotype, paratypes and referred specimens from the type locality). See also Figure 8.

S. brownei distinguishable from all species named above, with the possible exception of *S. antiquus*, by tapering of horizontal ramus of mandible towards front (see Diagnosis above).

Further distinguishable from *S. notabilis* and *S. orientalis*, and probably from *S. tindalei*, *S. antiquus* and *S. pales* (in which the holotypes are skull fragments) by smaller size, and from *S. andersoni* and *S. gilli* by larger size, of lower molars. Upper molars smaller in *S. brownei* than in *S. tindalei* and *S. antiquus*, and probably in *S. pales* (and *S. orientalis* and *S. notabilis*?), and larger than in *S. andersoni* and *S. gilli*.

Differs from *S. atlas* in that width of lower permanent premolar exceeds crown height, and lower molars show abundant fine crenulations. Differs from *S. oreas* in that lower permanent premolar longer than any molar (upper or lower), and much longer (averaging about 40%

longer) than first lower molar. Differs from *S. occidentalis* in that lower incisor much smaller and lower permanent premolar shorter (less than 16 mm.); upper permanent premolar probably also shorter, but upper and lower molars similar in size, to *S. occidentalis*.

Upper molars here attributed to *S. brownei* (see below) show anterior shelf divided by ridglet into smaller, smoother lingual portion and larger buccal portion with abundant fine crenulations, and median valley enclosed buccally by longitudinal low crest. Upper permanent premolars here attributed to *S. brownei* show marked vertical ridges on buccal faces, and most anterior lingual cusp nearly as prominent as most anterior buccal cusp.

For other mandibular and probable skull characteristics of *S. brownei*, see examples described in Tables 3 and 4 below.

Fig. 3.—Comparison of mandibular cheek teeth in *S. brownei* (63.2.51) and *S. occidentalis* (63.2.47) from Mammoth Cave, Western Australia. Both specimens juveniles from which deciduous premolars and milk molars have been removed, exposing unerupted permanent premolar. Note difference in morphology and length in permanent premolars, more pronounced fine crenulation on molars in *S. brownei*.

Sthenurus occidentalis Glauert 1910

Sthenurus occidentalis (partim) Glauert, 1910 (before Feb. 2nd) *Rec. West. Aust. Mus.* **1** : 31-36, pl. 5, figs. 6-7.

Holotype.—Western Australian Museum fossil vertebrate specimen 60.10.2, major portion of mandible lacking upper parts of coronoid and condylar regions; full adult dentition on both sides.

Described by Glauert (1910a) with photographs of right buccal and occlusal aspects ("Plate V, figs. 6 and 7", printed as separate plates). Collected by E. A. Le Souef in 1904 in two portions, later fitted together by L. Glauert ("The West Australian" Feb. 2nd, 1910, p. 4), the larger portion described by Glauert (1910b) with photographs of occlusal, left buccal and left lingual aspects (Plates 10-12).

Type locality.—Mammoth Cave, Western Australia, 34° 1½′ S, 115° 1½′ E—probably on margin of Glauert excavation, north-central in cave (Merrilees, Ph.D. dissertation).

Paratypes.—Descriptions of specimens by Glauert (1910a) and his internal Museum records do not permit certain recognition of all his paratypes nor of their precise location in Mammoth Cave. However, their location probably is near that of the holotype (Merrilees Ph.D. dissertation). Specimens 63.2.74 probably and 63.2.194 certainly are paratypes and certainly fall within my revised concept of *S. occidentalis*. Specimens 63.2.195-196 are paratypes and probably fall within my revised concept of *S. occidentalis*. Specimen 63.2.197 and some other juvenile specimens not now recognizable are paratypes but are referred by me to *S. brownei* sp. nov. See Discussion below.

Other specimens from Mammoth Cave, referred by me to S. occidentalis.—

(a) Mandibular specimens 61.7.57 (+ 63.2.83), 63.2.45, 63.2.47 (+ 63.2.67), 63.2.52-54, 63.2.56-62, 63.2.65-66, 63.2.68-71, 63.2.73, 63.2.75 (+ 63.2.92), 63.2.76-80, 63.2.85, 63.2.87-88, 63.2.91, 63.2.96-101, 63.2.102 (+ 63.2.114), 63.2.103-104, 63.2.115, 63.2.118, 63.2.161.

(b) Maxillary and premaxillary specimens 62.4.3-6, 62.4.8, 62.8.31, 63.2.119, 63.2.123, 63.2.125-132, 63.2.134, 63.2.138 (+ 61.7.58 + 63.2.136), 63.2.139, 63.2.142 (+ 63.2.137), 63.2.147, 63.2.149, 63.2.151-156, 63.2.162-164, 63.2.166, 63.2.168, 63.2.169 (+ 62.4.7), 63.2.170, 63.2.172-173, 63.2.175, 63.2.177-178, 63.2.180-181, 63.2.183-184, 63.2.186-190, 66.7.10-11, 66.8.7, 66.9.51.

(In the foregoing lists of specimens, numbers added in brackets refer to specimens catalogued separately but subsequently judged to derive from the same individual animal.)

Revised diagnosis.—Lower permanent premolar longer than in *S. brownei*, conspicuously longer than any molar. Lower incisor larger than *S. brownei* or *S. gilli*.

TABLE 3

Comparison of Western Australian Museum specimen 63.2.94 (holotype of S. brownei*) with 60.10.2 (holotype of* S. occidentalis*) from Mammoth Cave.*
(Both specimens show adult mandibular dentition. Measurements in mm)

	63.2.94	60.10.2 (Right side)
Depth incisor	9.5 (may be reduced by wear).	13.1
Incisor incumbency : angle between long axis of incisor and occlusal plane of cheek teeth	30—35° (i.e. more procumbent).	40—45° (i.e. more incumbent).
Upper aspects of symphysis immediately behind incisors	shallow U-shape.	deep V-shape.
Upper aspects of symphysis immediately behind genial pits	broad, gently sloping shelf.	narrow, steeply sloping shelf.
Length x width permanent premolar ; wear stage	14.7 x 9.9 ; III	16.8 x 9.7 ; II
Crown height permanent premolar (postero-lingual)	8.4	8.5
Form of permanent premolar ; occlusal surface	long lingual crest ; postero-buccal crest reaches further forward than half-way along tooth.	long lingual crest ; postero-buccal crest reaches forward about half-way along tooth.
Form of permanent premolar ; horizontal section near base of enamel	buccal embayment present but not marked ; projection in front of anterior cusp small.	marked buccal embayment ; extensive projection in front of anterior cusp.
Length x width first molar ; wear stage	10.8 x 9.2 ; M	9.9 x 8.8 ; B
Length x width second molar ; wear stage	11.5 x 9.9 ; E	11.1 x c. 9.7 ; B
Length x width third molar ; wear stage	12.0 x 10.3 ; B	11.4 x 10.1 ; B
Length x width fourth molar ; wear stage	11.2 x 10.4 ; B	10.2 x 10.0 ; B
M_3 protolophid : width near occlusal surface	10.0	9.2
M_3 protolophid : width near base of enamel	10.2	10.0
M_3 hypolophid : width near occlusal surface	10.1	9.0
M_3 hypolophid : width near base of enamel	10.2	9.9
Form of M_1 : transverse vertical section through hypolophid	sides converge downwards.	sides diverge downwards.
Form of molars : posterior cingulum	small but distinct shelf.	mere swelling near base of enamel.
Form of molars : minor ornamentation and links	present ; fore-link and mid-link weak.	present ; fore-link and mid-link very weak.
Vertical height of ramus below P_4—M_1 interspace	33	34
Vertical height of ramus immediately behind M_1	45	38 (L. side).
Position below which lower border of ramus descends lowest	posterior border of coronoid process.	immediately behind M_1.
Lowest point of masseteric crest	a little below level of molar alveoli.	below level of molar alveoli.
Lateral thickness of masseteric crest at lowest point	2	4½
Lateral thickness of anterior border of coronoid process at M_4 occlusal level	3	5
Antero-posterior length of masseteric fossa level with top of mandibular foramen	22	35
Maximum lateral width of lower rear part of ramus surrounding mandibular foramen	23	28
Crest bounding pterygoid fossa	terminates anteriorly in small sharp process ; deep sulcus between this process and small ridge diagonally placed on lingual face of horizontal ramus.	slight sulcus interrupts smooth confluence with lingual face of horizontal ramus.
Digastric sulcus, maximum forward extent	below anterior M_4.	below anterior M_2.
Posterior mental foramen	below anterior M_2.	below anterior M_2.

Lower molars show little or no posterior cingulum; wider at base of enamel than at transverse occlusal ridges. Lower permanent premolar with pronounced buccal embayment; postero-buccal crest curves inward towards lingual crest about half way along tooth.

Horizontal ramus of mandible about same depth behind M_4 as below P_4M_1 interspace, lowest part of masseteric crest falls far below level of molar alveoli, and thick; masseteric fossa (level with top of mandibular foramen) longer antero-posteriorly than *S. brownei*; crest bounding pterygoid fossa nearly confluent with lingual wall of horizontal ramus.

Comparison of S. occidentalis *with other species, and revised description.—*

(Same comparisons required as with *S. brownei* above.)

See illustrations of holotype of *S. occidentalis* provided by Glauert 1910a, b. See also Figures 3, 4 below (direct comparisons of lower and

TABLE 4

Comparison of Western Australian Museum specimen 63.2.198 (skull of Sthenurus brownei*) with 62.8.31 (skull of* S. occidentalis*) from Mammoth Cave.*

(The specimens represent juvenile animals, 63.2.198 being smaller than 62.8.31 and with M^4 not fully erupted. Measurements in mm.)

	63.2.198	62.8.31
Maximum diameter of root of left I^1 near enamel margin, perpendicular to long axis of tooth	7.0	10.0
Maximum diameter of root of left I^2 near enamel margin, perpedicular to long axis of tooth	4.4	4.3 (right)
Maximum diameter of root of left I^3 near enamel margin, perpendicular to long axis of tooth	7.6	c. 7.6 (right)
Minimum distance between alveolar margins of I^2 teeth of opposite sides	9.1	c. 10.3
I^3, lingual surface of crown	smooth	(I^3 not present)
Distance between alveolar margins of I^3 teeth of opposite sides, about central, internal margins	12.7	13.0
Incisive foramina, posterior endings	narrow slits	rounded
Premaxillary-maxillary sutures behind incisive foramina	project far backwards	end at foramina
Posterior palatal vacuities, anterior margins level with :—	posterior P^3	posterior DP^4
Length x width, and wear, of P^3 ; side measured	10.7 x 9.5, III ; R	10.8 x 9.6, III ; L
Length x width, and wear, of DP^4 ; side measured	10.1 x 10.5, M ; R	9.8 x 10.2, M ; L
Length x width, and wear, of P^4 ; side measured	16.2 x 12.4, I ; R	c. 18 x 13.0, I ; L
Form of P^3	many minor crenulations	few minor crenulations
Form of DP^4	many minor crenulations	few minor crenulations
Form of P^4—most anterior lingual and buccal cusps	lingual nearly as prominent as buccal	buccal far more prominent than lingual
Form of P^4—buccal face	strongly ridged	weakly ridged
Length x width, and wear, of M^1 ; side measured	11.1 x 10.3, E ; R	10.3 x 10.9, E ; L
Length x width, and wear, of M^2 ; side measured	12.0 x 11.0, B ; R	11.4 x 11.7, B ; L
Length x width, and wear, of M^3 ; side measured	12.1 x 11.2, B ; R	11.7 x 12.3, B ; L
Length x width, and wear, of M^4 ; side measured	c. 11.1 x 10.6, U ; R	11.1 x 11.6, B ; L
Form of molars—general	minor crenulations very prominent, especially in central valley	minor crenulations present, but more subdued than 63.2.198
Form of molars—anterior shelf	divided into smaller, smooth lingual portion and larger, buccal portion with prominent minor ridglets	undivided ; subdued ridglets throughout
Form of molars—central valley	enclosed buccally by longitudinal crest (also visible in DP^4)	M^4 partially closed buccally by low longitudinal crest, others open
Form of molars—posterior shelf, viewed in prone position	on buccal side, falls below anterior shelf of next succeeding molar	at no position lower than corresponding position on anterior shelf of next succeeding molar
Basisphenoid	long (c. 18)	short (c. 7)
Tympanic, ventral border	steeply sloping	almost horizontal
Tympano—zygomatic cell	large	small
Condyloid foramen, viewed in prone position	overhung by condyle	not overhung by condyle
Condyles, elongation, angle with vertical axis	c. 45°	c. 60°
Subsquamosal foramen	in shallow depression	in deep depression
Interparietal suture, rear portion	lies in deep depression between post-orbital crests	about same level as post-orbital crests
Fronto-parietal sutures	change direction abruptly from obliquely antero-posterior to lateral	curve smoothly round from obliquely antero-posterior to lateral
Orbit, minimum thickness at border of antero-ventral wall, level with infra-orbital foramen	2	6
Zygomatic process, anterior border descends opposite :—	posterior part of M^1	anterior part of M^1
Zygomatic process, anterior border near root	sharply ridged	rounded
Infra-orbital foramen	large, deeply recessed	small, opening from shallow concavity
Interpremaxillary suture, anterior portion	rises vertically above incisors, abruptly becoming horizontal	slopes upward and backward from incisors in smooth curve
Narial aperture, lower margin seen from in front	catenary curve	wide V shape
Maxillary-premaxillary suture, vertical ascent on external aspect of skull	opposite anterior ends of incisive foramina	opposite posterior ends of incisive foramina

Fig. 4.—Comparison of maxillary teeth in *S. brownei* (63.2.145) and *S. occidentalis* (62.4.4) from Mammoth Cave, Western Australia. Note low bucal crest enclosing central valley of M^2, ^{3} in 63.2.145.

probable upper cheek teeth in *S. occidentalis* and *S. brownei*), Fig. 7 (part of skull probably of *S. occidentalis*), and Table 2 (summary of tooth dimensions in holotype and specimens from same locality as holotype, referred by me to *S. occidentalis*).

Distinguishable from *S. notabilis* and *S. orientalis*, and probably from *S. tindalei*, *S. antiquus* and *S. pales* (in which the holotypes are skull fragments) by smaller size, and from *S. andersoni* and *S. gilli* by larger size, of lower molars. Upper molars smaller in *S. occidentalis* than in *S. tindalei*, *S. antiquus* and probably *S. pales* (also *S. orientalis* and *S. notabilis*?), and larger than in *S. andersoni* and *S. gilli*.

Differs from *S. atlas* in that width of lower permanent premolar exceeds crown height. Differs from *S. oreas* in that lower permanent premolar conspicuously longer than any molar (upper or lower), averaging 59% longer than first lower molar.

Differs from *S. brownei* in that lower incisor larger, lower permanent premolar longer (exceeds 16 mm.) and ramus about as deep below P_4-M_1 interspace as immediately behind M_4.

Differs from *S. orientalis* not only in having smaller (shorter and narrower) lower molars but in having lower permanent premolar longer relative to the lower molars. Lower permanent premolars of similar absolute lengths in *S. occidentalis* and *S. orientalis*.

Upper molars here attributed to *S. occidentalis* show anterior shelf more or less uniformly ornamented with subdued crenulations; crenu-

Fig. 5.—Skull of *Sthenurus brownei*, Mammoth Cave, Western Australia. Note thin crest forming anteroventral border of orbit, and sharp ridge forming anterior border of zygomatic process.

lations present elsewhere on occlusal faces of upper molars, but less prominent than on *S. brownei*. Upper permanent premolars here attributed to *S. occidentalis* show weak vertical ridges on buccal faces, and marked inequality between most anterior buccal and lingual cusps (buccal much more prominent).

For other mandibular and probable skull characteristics of *S. occidentalis*, see examples described in Tables 3 and 4.

Despite the fact that Tedford (1966) was not aware of the existence of two *Sthenurus* species from Mammoth Cave, his diagnosis and description (p. 33 to end of second paragraph p. 36) and illustrations (Figs. 11, 12) of *S. occidentalis* require little amendment. Deletion of the comment "The median valley is closed labially in unworn teeth by a prominent thin crest from the paracone" (p. 34) and alteration of the comment on the masseteric crest (p. 33 and also p. 61) to read "masseteric crest descends below level of alveolar border" would make Tedford's description of *S. occidentalis* applicable to my revised concept of it.

Discussion

Specimen 63.2.94 is chosen as the holotype of *S. brownei* partly because the laminated structure of the material originally encrusting much of the specimen suggests that it may have come from stratigraphically higher parts of the deposit(as did the holotype of *S. occidentalis*), partly because the specimen could not have been used by Glauert (1910) to formulate his concept of *"S. occidentalis"* (since its teeth were then obscured by matrix except for part of the incisor) and partly because it represents the same part of an animal of about the same dental age as the holotype of *S. occidentalis*. The "diagnoses" and "comparisons with other species" above of *S. brownei* and *S. occidentalis* are based mainly on the respective holotypes.

There is thus little doubt that mandibular specimens bearing permanent premolars have been assigned correctly to one or the other Mammoth Cave species, and such specimens have been designated above as paratypes in the case of *S. brownei*. But there must be some doubt about mandibular specimens which do not show permanent premolars, and considerable doubt about the specific identity of any skull fragment, since there is no direct evidence associating any skull with any mandibular specimen. Mandibular specimens lacking the permanent premolar and all skull fragments have been considered, therefore, not to have the status of paratypes, but merely of specimens referred to their respective species with some measure of uncertainty, in spite of coming (with the possible exception of 10087—see note above) from the same circumscribed deposit as the holotypes and paratypes.

Table 3 above compares the holotypes of *S. brownei* and *S. occidentalis*, and Table 4 compares skull structures in the two most complete *Sthenurus* skulls recovered from Mammoth Cave. Table 4 records many differences between these skulls which cannot be attributed to differences of growth, since the animals concerned were of similar dental age. (Dental wear designations in Tables 3 and 4 are as used by Tedford 1966, pp. 4, 5.)

None of the numerous other *Sthenurus* skull fragments from Mammoth Cave shows all the diagnostic structures listed in Table 4, but there is little difficulty in assigning nearly all such specimens either to a group resembling skull 63.2.198 or to a group resembling skull 62.8.31, and these are the groups listed above under *S. brownei* and *S. occidentalis* respectively.

My reasons for assigning skull 63.2.198 and the fragments resembling it to *S. brownei* and skull 62.8.31 and the more numerous skull fragments resembling it to *S. occidentalis* are as follows. Skull 63.2.198 has a shorter permanent premolar with lingual and buccal crests of approximately equal height, and this is more consistent with the lower permanent premolars characteristic of *S. brownei* than with the longer, slightly more sectorial lower permanent premolars characteristic of *S. occidentalis*, in which the lingual crests greatly overshadow the buccal crests in P_4 teeth. The ratio of juveniles (with P^4 not yet erupted) to adults in the group resembling 63.2.198 is much higher than in the group resembling 62.8.31, and this too is more consistent with the mandibular specimens of *S. brownei* than *S. occidentalis*. There are at least 16 individuals represented in the 62.8.31 skull group, but it is possible to estimate the dental age in only 14 of these indivduals; of these 14 only 5 are juveniles. At least 9 individuals are represented in the 63.2.198 skull group, and of these 9, 6 are juveniles. Among mandibular specimens, *S. occidentalis* is represented by at least 15 individuals of which 13 are of determinable dental age, only 2 of these being juveniles; whereas of at least 13 individuals of *S. brownei*, all of determinable dental age, 7 are juveniles. Skull 62.8.31 is of generally more robust construction than skull 63.2.198; for example, the antero-ventral borders of the orbits are thicker and more rounded in 62.8.31. Mandibles of *S. occidentalis* appear to be rather more robust than those of *S. brownei*; for example, the masseteric crest is thicker at its lowest point in *S. occidentalis* than in *S. brownei*. On grounds of greater robustness, it is perhaps reasonable to assign skull 62.8.31 to *S. occidentalis* and 63.2.198 to *S. brownei*.

Skull 63.2.198 (*S. brownei*) shows only right I^2 and I^3 and left I^2 of the incisor row, the other incisors being represented only by broken stumps in their sockets. Skull 62.8.31 (*S. occidentalis*) shows the broken stump of I^1 and I^2 of both sides, and empty alveoli of I^3 of both sides. Isolated upper incisors, and premaxillary specimens showing one or more incisors, are not readily separable into two clear-cut groups. Consequently upper incisors cannot be identified with confidence as *S. brownei* or *S. occidentalis*.

However, the I^3 remaining on 63.2.198 is of a strap-like form not unlike that illustrated for *S. gilli* by Merrilees (1965 Fig.6), and is smooth on the lingual face, while the I^2 teeth remaining on 63.2.198 are rather small by comparison with other I^2 teeth of *Sthenurus* from Mammoth Cave. It is reasonable to suggest that the upper incisor row in *S. brownei* should be smaller than that of *S. occidentalis* by analogy with the lower incisors, which are smaller in *S. brownei*. A complete set of upper incisors is preserved on specimen

63.2.144, which appears from the fit of broken edges to represent the front part of the same skull as maxillary specimen 63.2.145. Specimen 63.2.145 shows a short P^4, and $M^{1,2,3}$ each with prominent minor ridglets, a divided anterior shelf, and a posterior shelf falling below the level of the anterior shelf of the next succeeding molar, and probably represents *S. brownei*. I assume that 63.2.144 also represents *S. brownei*, and this identification is also suggested by characters of the specimen itself such as vertical ascent of the premaxillary-maxillary suture opposite the forward part of the incisive foramen or abrupt change from vertical to horizontal in the profile below the narial aperture.

Specimen 63.2.144 may be contrasted with 63.2.152 in the ways discussed below, and I assume from these contrasts that 63.2.152 represents *S. occidentalis*. Other specimens bearing sthenurine upper incisors have been separated into two groups according to their resemblance to 63.2.144 or to 63.2.152.

The lingual face of I^3 in 63.2.144 differs from that of 63.2.152 both in profile and in the texture of the surface. I^3 in 63.2.144 is smooth on the lingual face, and the maximum width of the tooth is about half way down the crown; I^3 in 63.2.152 shows many minor crenulations, a pronounced fold in the enamel of the antero-lingual "corner", and a maximum width close to the occlusal edge. Viewed in the prone position, I^3 in 63.2.144 shows a slightly sigmoid section, with a slight lingual in-turning of the anterior border and a slight buccal out-turning of the posterior border. On the other hand, I^3 in 63.2.152 shows a more evenly curved section, with buccal convexity. In both specimens, both in prone and in buccal views, a thickening of I^3 along its antero-buccal border is evident. I^1 and I^2 are larger in 63.2.152 than in 63.2.144, but otherwise similar.

Early observations on the Sthenurus sample from Mammoth Cave

The holotype of *S. occidentalis* and at least one other *Sthenurus* specimen appear to have been collected by E. A. Le Souef very soon after fossil mammals were first discovered in Mammoth Cave in 1904. Le Souef identified his find as a new variety of *Sthenurus atlas*. He used the name *S. atlas hacketti* in a report made by him in 1904 or 1905 to the Caves Board, but this name appears not to have been published until Feb. 5th 1910, when Le Souef quoted extracts from his report in a letter to the Editor of "The West Australian" (a daily newspaper). Le Souef's letter appears to have been prompted by an article in the same newspaper three days earlier (Feb. 2nd 1910), which article mentions "the first volume of the Records of the Museum and Art Gallery", carrying Glauert's description of *S. occidentalis*. I accept Glauert's publication of the name *S. occidentalis* as antedating Le Souef's *S. atlas hacketti* by a few days. Woodward (1909) mentions Glauert's intention to use the name *S. occidentalis*, probably for 60.10.2, but gives no description; Glauert (1909) mentions but does not name his new species. Glauert appears to have described the incomplete mandible (part of 60.10.2—see above) in

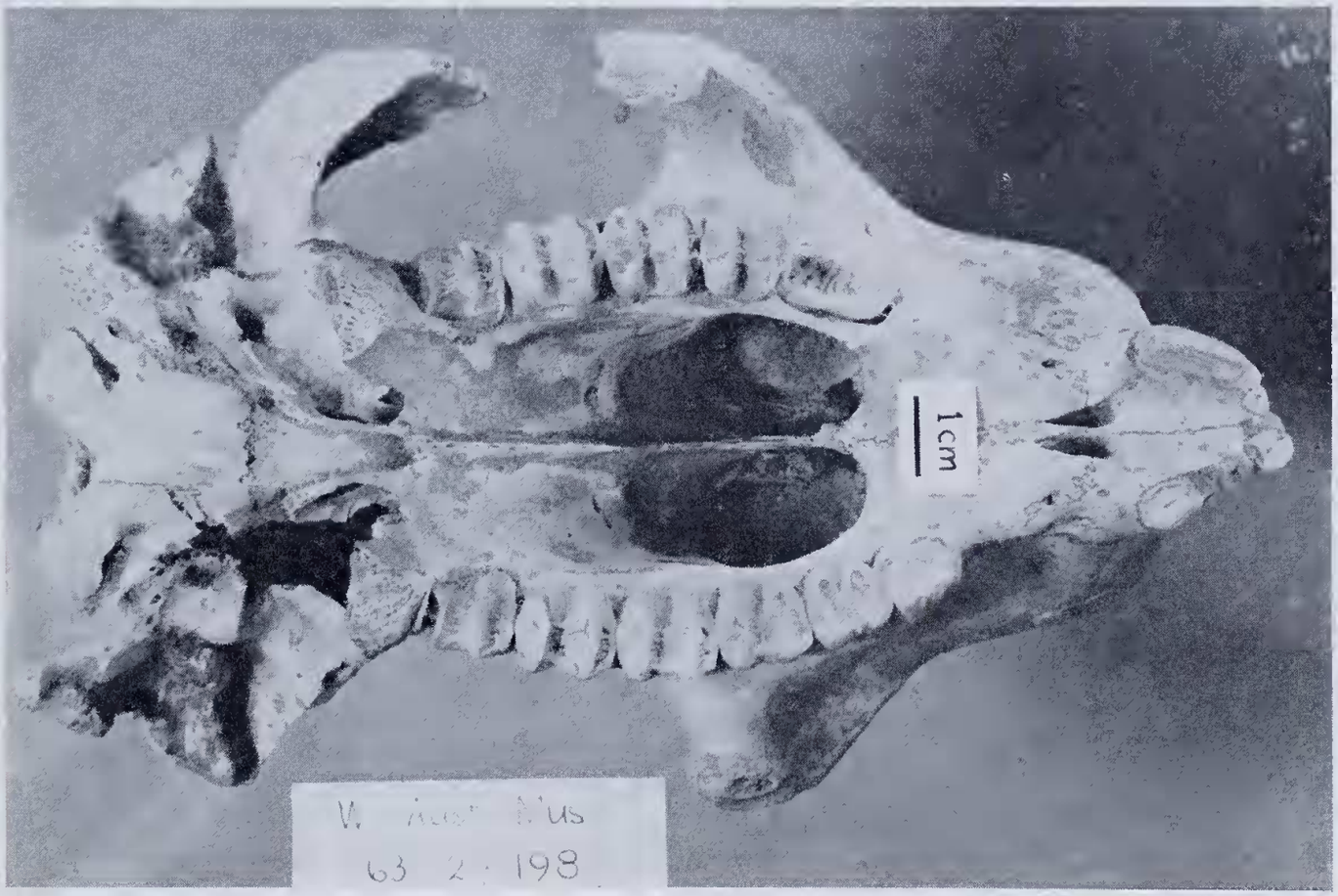

Fig. 6.—Skull of *Sthenurus brownei*, Mammoth Cave, Western Australia. Right permanent premolar exposed by removing deciduous premolar and milk molar. (Same specimen shown by Anderson 1932, Plate 45, Fig. 1.)

a report to the Caves Board, part of which report also was published in 1910, but not before March 21st, since that date appears on the Government Geologist's "Prefatory Note" to Bulletin 36, Geological Survey of Western Australia, which carried Glauert's description. Le Souef's report to the Caves Board, including the name *Sthenurus hacketti,* was quoted again in "The West Australian", Feb. 21st 1914; but *S. atlas hacketti* (or *S. hacketti*) appears not to have been used since then.

Glauert's description of *S. occidentalis* (1910a —Rec. West. Aust. Mus. 1) clearly designates the specimen now catalogued as 60.10.2 as the holotype, and mentions also some other specimens, not all of which can now be recognized with certainty. However, it is probable that some of these specimens (63.2.194-196, 63.2.74) are referable to *S. occidentalis* as revised by me, while some (63.2.197 and some juvenile specimens) are referable to *S. brownei.* In fact,

TABLE 5

Relative magnitudes of differences in tooth dimensions between sexes in some modern macropod samples and between two groups in the fossil* Sthenurus *sample from Mammoth Cave.*

Sample	Tooth dimension examined	Difference between means within sample mm	Mean of females or *S. brownei* mm	Magnitude of difference %
Protemnodon bicolor	Length P^4	0.30	9.60	3.1
Bettongia penicillata	Width M^1	0.21	4.03	5.2
Protemnodon agilis	Width M^4	0.36	6.33	5.7
Macropus robustus	Width M^1	0.50	7.28	6.9
Macropus robustus	Length P^4	0.70	7.67	9.1
†*Megaleia rufa*	Width M^1	0.59	7.56	7.8
†*Megaleia rufa*	Length P^4	0.72	6.96	10.3
Sthenurus, Mammoth Cave	Length P^4	1.65	15.93	10.4
Sthenurus, Mammoth Cave	Length P_4	2.32	14.42	16.1

* Relative magnitudes stated as percentages : difference in arithmetic mean for stated dimensions between groups within sample as proportion of mean for females or for " small-toothed " group (i.e. *S. brownei*) in *Sthenurus.*

† Data from Sharman, Frith and Calaby, 1964.

TABLE 6

Tooth dimensions in specimens of Sthenurus brownei *from Strong's Cave and Wanneroo, Western Australia.*

Length x width, upper permanent premolar ; side
66.11.62 Strong's Cave c. 14.5 x 12.0 ; L
65.9.59 Strong's Cave c. 15 x c. 12 ; L
Depth, lower incisor ; side
65.6.45 Strong's Cave 9.0 ; L
65.6.61 Strong's Cave 10.0 ; R
65.6.65 Strong's Cave 9.6 ; R
Length x width, mandibular cheek teeth ; side
61.11.64 Strong's Cave P_3 c. 8.6 x c. 7.6 ; L
61.11.63 Strong's Cave P_4 c. 14.6 x c. 10.2 ; L
65. 9.28 Strong's Cave M_2 10.4 x 9.5 ; R
65. 9.28 Strong's Cave M_3 11.0 x 9.9 ; R
61. 6. 2 Wanneroo P_3 8.3 x 7.5 ; R
61. 6. 2 Wanneroo DP_4 8.6 x 8.3 ; R
61. 6. 2 Wanneroo P_4 15.2 x 9.6 ; L (excavated)
61. 6. 2 Wanneroo M_1 10.0 x 8.8 ; R
61. 6. 2 Wanneroo M_2 11.6 x 9.9 ; R
66.10.14 Wanneroo P_4 13.5 x 8.6 ; R (excavated)
66.10.14 Wanneroo M_1 c. 9.6 x c. 8 ; L
66.10.14 Wanneroo M_2 10.8 x 9.4 ; L
66.10.14 Wanneroo M_3 11.5 x 10.1 ; L
66.10.14 Wanneroo M_4 c. 11 x 9.8 ; R

Glauert mentions characters that I consider diagnostic of *S. brownei*; referring probably to 63.2.197, Glauert states that "The ramus . . . is more slender and has a decided angle at the posterior lower end of the horizontal ramus in place of the graceful curve that characterises *S. occidentalis.*" However, he adds that this is a "character which loses its sharpness as the animal increases in size", whereas the holotype of *S. brownei* comes from an adult animal but still shows this character quite clearly. Elsewhere, Glauert (1910b) draws attention to differences between the permanent premolar in specimen 10087 and the holotype of *S. occidentalis,* but dismisses these differences as individual variations.

Anderson (1932) reports his examination of two skulls from Mammoth Cave, his specimen A (now catalogued as 62.8.31, *S. occidentalis*) and specimen B (now catalogued as 63.2.198, *S. brownei,* figured by Anderson, Plate 45, Fig.1). Anderson draws attention to differences between 62.8.31 and 63.2.198, but does not suggest that they represent distinct species.

Anderson (1932) also describes and figures a specimen from King Island, his specimen C, from the collection of the Queen Victoria Museum and Art Gallery, Launceston. I have been able to examine this specimen, and have concluded that it resembles 62.8.31 more closely than 63.2.198, although it is rather small. Glauert (1948) reproduces what appears to be a reversed print of Anderson's (1932) Plate 46, Figure 1 (showing the King Island specimen) as part of a discussion on fossils from Mammoth Cave; Glauert's (1948) plate, like Anderson's original, is labelled *S. occidentalis.*

Possiblity of sexual dimorphism in the Mammoth Cave sample of Sthenurus

Sexual dimorphism in various skeletal elements, even in tooth dimensions, is well-known in mammals; for example Kurtén and Rausch (1959) demonstrate significant differences between the sexes in three tooth dimensions in the Alaskan wolverine (*Gulo gulo*) and Ride (1964) similarly in five tooth dimensions in the modern Tasmanian "wolf" or "tiger" (*Thylacinus cynocephalus*). I have examined various samples of modern macropods for sexual dimorphism in tooth dimensions, and have found some significant differences; also I have shown that data on the modern red kangaroo (*Megaleia rufa*—see Ride 1962) published by Sharman, Frith and Calaby (1964 Table 4) reveal significant differences between the sexes at least in respect of posterior width of P^4, length of P^4 and width of M^1. However, the magnitude of these differences between the sexes in modern samples in no case approaches the magnitude of the difference between lengths of the lower permanent premolars in the two groups discernible in the Mammoth Cave fossil sample of *Sthenurus.* See Table 5. Furthermore, I know of no example of sexual dimorphism in tooth form such as those clearly shown by lower permanent premolars in the two kinds of *Sthenurus* from Mammoth Cave, or somewhat less clearly by the upper permanent premolars or upper or lower molars. Nor am I aware of any example of sexual dimorphism in so many non-dental structures as those listed above for the Mammoth Cave *Sthenurus.*

Fig. 7.—Part of skull of *Sthenurus occidentalis*, Mammoth Cave, Western Australia. Left permanent premolar exposed by removing deciduous premolar and milk molar. Compare with *S. brownei*, Fig. 6. Note difference in form of incisive foramina, and difference in forward extent of palatal vacuities.

Thus I conclude that the observed differences between the two groups of *Sthenurus* in Mammoth Cave far exceed sex differences demonstrable in any macropod, or indeed in any mammal sample known to me. A fuller account of the investigations upon which this conclusion is based is given elsewhere (Merrilees, Ph.D. dissertation). If the observed differences within the Mammoth Cave sample are not sex differences, the only other reasonable postulate is that they are specific differences.

Subgeneric status of S. brownei and S. occidentalis

Tedford (1966) suggests that subgeneric distinction should be made between species with procumbent lower incisors, narrow, trenchant premolars, narrow molars etc. (such as *S. atlas*) and species with incumbent lower incisors, massive premolars, wide molars etc. (such as *S. orientalis*). Both *S. occidentalis* in the revised sense and *S. brownei* fall into the latter group, for which Tedford proposes the subgeneric name *Simosthenurus*.

Sthenurus in Strong's Cave

Strong's Cave is in the same series of calcareous aeolianites as Mammoth Cave, but about 7 miles further south. Cook (1963) suggests that the Strong's Cave fauna is younger than that of Mammoth Cave, and I have shown (Merrilees, Ph.D. dissertation) that the Strong's Cave fossiliferous deposits may be younger than those of Mammoth Cave.

W. Aust. Mus. specimen 61.11.10 is one of several *Sthenurus* specimens recovered from the bed of a stream traversing Strong's Cave (Cook 1963); it is a left lower permanent premolar with a fully formed crown and portions of the roots, from which the posterior roots and part of the crown have been removed by stream erosion. Its length cannot be recorded with certainty, but is about 15.9 mm; its width is 10.2 mm. Thus it is shorter than any Mammoth Cave specimen of *S. occidentalis* and longer than any Mammoth Cave specimen of *S. brownei*. However, it closely resembles the Mammoth Cave sample of *S. occidentalis* in form, and in spite of its shortness, I ascribe it to *S. occidentalis*. It is the only specimen of this species so far recovered from Strong's Cave.

On the other hand, several specimens from Strong's Cave, though all fragmentary, are referable with confidence to *S. brownei*; these are 61.11.62-63, 65.6.45, 65.6.61, 65.6.65, 65.9.28, 65.9.59. See Table 6. Specimens 61.11.64, 65.6.58 and 65.6.63 are probably *S. brownei*, while

various other fragmentary specimens (e.g. 65.9.96), obviously of *Sthenurus*, cannot be specifically identified.

S. brownei from Wanneroo

Two pieces of bone-bearing granular calcareous material were presented to the Western Australian Museum in 1937 by Mr. A. Skroza. The locality from which these specimens came appears not to have been investigated nor even recorded in detail; however, it is known to have been a limestone quarry in the Wanneroo district, on the northern outskirts of the Perth metropolitan region. The specimens can be assumed, therefore, to have come from the aeolianite series informally known as the Coastal Limestone. One of the lumps has been subjected to acetic and monochloroacetic acid treatment, and shown to contain numerous bone fragments, including two different macropodids and possibly a small reptile; so heterogeneous a material may represent an old cave fill cut into by quarry operations. The Coastal Limestone itself is generally considerd to be of late Pleistocene age (Smith 1963), and cave deposits within it may be considerably younger; it is therefore safe to assume that the Wanneroo specimens are of late Quaternary age.

The Wanneroo specimen now catalogued as 61.6.2 shows the central portions of right and left mandibular rami of a juvenile *Sthenurus*, almost certainly two sides of the same mandible. It was identified as *S. occidentalis* by L. Glauert in 1937, but I have extracted the unerupted permanent premolar from the left side and this shows it to be *S. brownei*. The molars and milk molars in this specimen are consistent in morphology and size with the Mammoth Cave sample of *S. brownei*, but the deciduous premolars are shorter. The excavated left permanent premolar shows a small supernumary root on the lingual side between the large anterior and posterior roots.

Acid preparation of the other Wanneroo lump has revealed a mandible (66.10.14) with the two rami still in contact, very little distorted from the life position. It lacks both incisors, the coronoid and condylar regions of both sides, and the deciduous premolars and milk molars of both sides, the unerupted permanent premolars both being exposed. The first three molars of the right side are extensively damaged. See Figure 8. In form, the permanent premolars, the molars, and the masseteric crest are very similar to the Mammoth Cave sample of *S. brownei*, and the length of the permanent premolar and the first three molars, and the widths of the second and third molars fall within the range of variation of the Mammoth Cave sample. However, the permanent premolar and the first molar are narrower than in any Mammoth Cave specimen of *S. brownei*, and the fourth molar is both narrower and slightly shorter. See Table 6.

Fig. 8.—*S. brownei* from Wanneroo, near Perth. W. Aust. Mus. 66.10.14.

I conclude that *S. brownei* once lived at Wanneroo, but that there may have been some tendency to smaller teeth in the Wanneroo than in the Mammoth Cave populations.

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